SIGNIFICANCE OF VISITS BY HACKBERRY BUTTERFLIES (NYMPHALIDAE: ASTEROCAMPA) TO FLOWERS

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ABSTRACT. Behavioral studies were conducted on hackberry butterflies (Asterocampa spp.) in central Texas as to their visitations to certain flowers. The butterflies were observed most abundantly on snakewood flowers (Colubrina texensis). A higher percentage of females were counted during sampling. It is speculated that Asterocampa spp., especially females, visit flowers which serve as a nitrogen source and do not require the carbohydrate-rich nectar sources of most other flowers.

Visits by rhopaloceran species to angiospermous flowers are well known even to laymen. However, as any knowledgeable lepidopterist is aware, some species are rarely or never observed at flowers. One group of butterflies generally believed not to visit flowers are the hackberry butterflies of the nymphalid genus Asterocampa. Howe (1975: 113) states that "they do not visit flowers but feed on decaying material-rotting fruit, fermenting tree sap, animal excrement and carcasses." No record of Asterocampa visiting flowers was known to Shields (1972) who reviewed butterfly flower visitation records. The most extensive published account of the life history account of any Asterocampa appears to be that of A. celtis (Langlois & Langlois, 1964). Adults were observed feeding at wet mud and fruit (mulberries and cherries). Kimball (1965) recounted observations of Asterocampa spp. feeding at rotton persimmons and oozing hackberry trees. A. clyton and A. celtis have been observed feeding at pig carrion in a state of "advanced decay" (Payne & King, 1969). Visits to waterholes in Arizona by A. celtis were observed by Bauer (1953). In Arizona, A. leila has been observed feeding at covote feces which contained much Opuntia fruit; they were never observed at flowers or mud puddles (Austin, 1977). In the eastern United States, Shapiro (1966) reported that A. celtis was "never seen . . . on flowers" while A. cluton were "occasionally seen clustered on over-ripe fruit." The only reference to Asterocampa on flowers that I have found is Scott and Scott (1980), who report that A. celtis in Colorado "rarely feed on flowers (Jamesia, etc.) but often feed on sap especially of willows and occasionally feed on mud or on Rubus berries." Kimball (pers. comm.), however, says he has observed Asterocampa spp. visiting a variety of flowers on several occasions. The purpose of this communication is to document significant visitations by Asterocampa spp. to angiospermous flowers and to elucidate environmental factors which resulted in this activity.

OBSERVATIONS

All observations discussed below, unless otherwise so indicated, were made in McKinney Falls State Park, Travis Co., Texas, just southeast of Austin. The specific area was an upland flat above the left bank of Onion Creek. Shallow soil covers the underlying Pflugerville Limestone (Upper Cretaceous: Gulf Series) except for isolated areas and the scarp where bedrock is exposed. Three vegetational associations are present at the site. The woodland consists of cedar elm, Ulmus crassifolia Nutt., with an occasional plateau live oak, Quercus fusiformis Small. A meadowlike open area is dominated by small bur-clover, Medicago minima (L.) L. and yellow stonecrop, Sedum nuttalianum Rof. A thicket association occurs at certain woodland edges and the scarp of the upland flat. Dominant shrubs of this thicket are snakewood. Colubrina texensis (T. & G.) Gray; Texas persimmon, Diospyros texana Scheele; spring herald, Forestierra pubescens Nutt.; and pink cat-claw, Mimosa borealis Gray. The only hackberry occurring in this immediate area are seedling, sapling and small shrubby netleaf hackberry, Celtis reticulata Torr. Approximately 50 m from the study site, treesize (to 8 m) individuals of both C. reticulata and Texas sugarberry, Celtis laevigata Willd. are present.

Observations on the study site were initiated on 7 March 1977 in connection with studies on other rhopalocera. An occasional Asterocampa was observed as early as 19 April when one fresh specimen of A. antonia (Edwards) was observed. Open flowers of snakewood were initially observed on 18 April. Moderate numbers of this species and A. texana (Skimmer) were observed feeding at flowers of Colubrina (Rhamnaceae) as early as 25 April (see Table 1). Flowers of snakewood are rather inconspicuous, being about 5 mm in diameter. The reduced petals form a yellowish five-pointed star surrounding a central green disc. Subsequently, for over two weeks adults of both species were observed at snakewood flowers. Last observed Asterocampa feeding at snakewood flowers was 10 May, although open flowers persisted through at least 19 May at this site. Apparent age of the butterflies was quite variable. All of the A. texana were fresh in appearance, although an age of one or two weeks is not unlikely. Adults of A. antonia varied from fresh to worn, very tattered adults. These tattered A. antonia were predominantly males.

Detailed behavioral observations of these butterflies were recorded. A butterfly at a snakewood flower was always observed to be moving its proboscis over the surface of the bowl of the flower. Nectar was not the object of this behavior. Unidentified substances, possibly including rich amounts of various amino acids, were obtained from the green

	A. antonia		A. texana	
	ð	ę	ð	ę
25 April		3:0*		0:1
26 April	3:1	5:0		1:1
29 April	0:1	0:3		2:0
6 May	_	1:0	1:0	1:0
10 May	—		_	1:0
Total	3:2	9:3	1:0	5:1

TABLE 1. Asterocampa observed at snakewood (Colubring texensis) flowers in 1977.

2 total-14:4; ö total-4:2; A. a.-12:5; A. t.-6:1.
* At flower: not at flower. Butterflies counted as "at flower" only if proboscis observed extended to disk of flower.

central disk. That significant amounts of amino acids may be available from snakewood flowers is indicated by the presence of carrion and dung flies at these flowers. Flowers attracting such flies must utilize high-level amino acid solutions in order to lure them away from their normal food sources which are naturally high in nitrogen (Baker & Baker, 1973a, b, 1975). All butterflies listed in Table 1 were observed to perform such behavior. During such activities neither feet nor antennae of Asterocampa touched the flower. Detection of the flower is apparently made visually with verification involving the highly flexible tip of the proboscis. Occasionally, the antennae are flexed up and down in unison, but no physical contact of the antennae was made with the flower. Possibly olfactory receptors in the antennae are receptive to chemicals emanating from the flowers. Movement from flower to flower was accomplished by walking along branches.

As only the proboscis of Asterocampa comes into contact with the flower, these butterflies are unlikely to be effective pollinators. From this standpoint, Asterocampa spp. can be considered to be "cheaters" or nutrient-thieving flower visitors (Heinrich & Raven, 1972), because they do not participate in pollen transport. Legitimate flower visitors (actual pollinators) included at least two paper wasps (Polistes annularis and P. apacheanus), 2 tachinid fly species, 1 ichneumon wasp, 1 muscid fly, 2 syrphid fly species, 1 conopid fly, honey bees (Apis mellifera L.) and 1 blow fly.

A number of other rhopaloceran species visited snakewood flowers, while several butterflies present in the area were never observed visiting these flowers (Table 2). Examination of Table 2 reveals a definite dichotomy between two classes of butterflies-those species which visit snakewood flowers and those that don't. That this is an ecologically significant dichotomy is remarkably demonstrated by the behavior of pollinating agents of snakewood and of balsam gourd, Ibervillea lindheimeri (Gray) Greene, a vine growing upon snakewood. Both plants

Species observed at snakewood flowers	Species at other flowers	
Atlides halesus estesi Clench Panthiades m-album (Bdv. & Lec.) Strymon melinus franki Field Libytheana bachmanii larvata (Strecker) Asterocampa antonia (W. H. Edwards) Asterocampa texana (Skinner) Vanessa atalanta rubria (Fruhstorfer)	Erynnis funeralis (Scudder & Burgess) Battus philenor philenor (Linnaeus) Phoebis sennae marcellina (Cramer) Abaeis nicippe (Cramer) Nathalis iole Boisduval Chlosyne lacinia adjutrix Scudder Agraulis vanillae incarnata (Riley) Danaus plexippus plexippus (Linnaeus) Danaus gilippus strigosus (Bates)	

TABLE 2. Rhopalocera observed during survey.

were blooming simultaneously, but pollinators of the two plants formed two mutually exclusive groups. *Asterocampa* and other visitors to snakewood flowers totally ignored balsam gourd flowers, while visitors to balsam gourd flowers (e.g., the butterfly, *Abaeis nicippe* Cramer, and a bumblebee, *Bombus* sp.) totally ignored snakewood flowers. Flowers of the two species were no more than five centimeters from each other.

Although Asterocampa were found abundantly on snakewood flowers, a limited number of other food sources were noted. On 29 April one female A. antonia was observed on pencil cactus, Opuntia leptocaulis DC.; the proboscis of this individual was actively probing at the internodal joints of this plant. On 10 May a female A. texana alit on my arm, extended its proboscis and probed along the skin surface. On this same day one male A. texana and one female A. antonia were observed visiting flowers of Canada garlic, Allium canadense L. var. canadense. On 13 May one male A. antonia was observed feeding at flowers of this same plant. On this same day one female A. texana was observed feeding at mud. On 20 May one male and one female were observed feeding at flowers of Acacia angutissima (Mill.) O. Ktze. var. hirta (Nutt.) B. L. Robinson.

One female A. texana was observed feeding on rotting fruit of purple leaf plum (Prunus cerasifera Ehrh. var. pissardii Koehne) in a residential yard in Austin. This butterfly appeared to be using its antennae to help locate fruit. The antennae were flexed up and down on the surface of the fruit in unison and were even whirled in complete circles in front of the body. However, widespread probing at the fruit with the proboscis was also observed.

Most blossoms present during those observations were ignored by Asterocampa, however. These included Medicago minima (L.) L., Sedum nuttalianum Rof., Lesquerella recurvata (Gray) Wats., Gaillardia pulchella Foug., Tradescantia ohioensis Rof., Phacelia congesta Hook., Cooperia drummondii Herb., Torilus nodosa (L.) Goert. and Zexmenia hispida (H.B.K.) Gray. Of particular interest were observations of two female A. texana which were observed landing on flowering inflorescences of P. congesta after they were "frightened" away from snakewood flowers (one individual disturbed by Polistes apacheanus, one by author). Each butterfly began investigating the P. congesta inflorescence with its proboscis; this behavior did not last more than two or three seconds as the butterflies appeared to be almost repelled by some characteristic of these flowers. The butterflies flew off to a branch of snakewood following this behavior.

DISCUSSION AND CONCLUSION

Of vital importance to the elucidation of the significance of flower visitation by Asterocampa is the preponderance of females in the samples observed. Of twenty-four butterflies actually verified to be feeding at snakewood flowers, eighteen or 75.0% were females. Normally, samples of butterflies from flowers yield a preponderance of males. However, these species are obtaining mostly carbohydrate from their nectar sources, although nectar of butterfly flowers are often fairly rich in amino acids (Baker & Baker, 1973b). Adult protein requirements are relatively low in these species, because nearly-sufficient amounts of nitrogen are obtained during its larval development.

Some butterfly larvae, however, are probably not able to store sufficient nitrogen for reproductive efforts because of difficulty in extracting nitrogen from foodplant material. The phytochemical defense of many tree species involves the production of "quantitative" poisonous substances, e.g., tannins, resins and silicates (Feeny, 1976). Owen (1959) observed that a British saturid butterfly, Pararge algeria (L.) rarely visits flowers; whereas, a congeneric species, P. megera (L.), frequently visits flowers. This was explained by habitat selection, the former species confined to woodlands and the latter to open areas, presumably because of habitat restriction of larval foodplant. Such an explanation may well be valid in the above case but does not hold for Asterocampa. While the Celtis utilized as larval foodplants occur in woodlands, these woodlands are open associations and in no way form closed canopies except under certain conditions; carbohydrate-rich nectar sources are nearly always nearby. Lack of visits by Asterocampa to showy, "typical butterfly" flowers (see list in text above), are caused by a lack of certain nutrients required by adult Asterocampa, especially females.

Quite possibly, Asterocampa, because it feeds as a larva on an "apparent" foodplant (see Feeny, 1976), suffers from a nitrogen-deficient larval diet. As a result, the imago would have to acquire sufficient nitrogen in order to reproduce. As the female contributes more protoplasm to the eggs which initiate the next generation, nitrogen requirements for adult female Asterocampa would be expected to be higher than requirements for male Asterocampa. As females would then spend more time obtaining nitrogen, one would expect to find more females than males in a given time period at a nitrogen source, e.g., flowers of Colubrina texensis or snakewood. However, certain differences in adult energy budgets of male and female butterflies are known (Adler, 1982).

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